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RESEARCH ARTICLE

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Behavioural change during dispersal and its relationship to survival and reproduction in a cooperative breeder

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Abstract

1. The ability of dispersing individuals to adjust their behaviour to changing conditions is instrumental in overcoming challenges and reducing dispersal costs, consequently increasing overall dispersal success. Understanding how dispersers' behaviour and physiology change during the dispersal process, and how they differ from resident individuals, can shed light on the mechanisms by which dispersers increase survival and maximise reproduction.
2. By analysing individual behaviour and concentrations of faecal glucocorticoid metabolites (fGCM), a stress-associated biomarker, we sought to identify the proximate causes behind differences in survival and reproduction between dispersing and resident meerkats *Suricata suricatta*.
3. We used data collected on 67 dispersing and 108 resident females to investigate (a) which individual, social and environmental factors are correlated to foraging and vigilance, and whether the role of such factors differs among dispersal phases, and between dispersers and residents; (b) how time allocated to either foraging or vigilance correlated to survival in dispersers and residents and (c) the link between aggression and change in fGCM concentration, and their relationship with reproductive rates in dispersing groups and resident groups with either long-established or newly established dominant females.
4. Time allocated to foraging increased across dispersal phases, whereas time allocated to vigilance decreased. Time allocated to foraging and vigilance correlated positively and negatively, respectively, with dispersers' group size. We did not find a group size effect for residents. High proportions of time allocated to foraging correlated with high survival, and more so in dispersers, suggesting that maintaining good physical condition may reduce mortality during dispersal. Furthermore, while subordinate individuals rarely reproduced in resident groups, the conception rate of subordinates in newly formed dispersing groups was equal to that of their dominant individuals. Mirroring conception rates, in resident groups, fGCM

concentrations were lower in subordinates than in dominants, whereas in disperser groups, fGCM concentrations did not differ between subordinates and dominants.
5. Our results, which highlight the relationship between behavioural and physiological factors and demographic rates, provide insights into some of the mechanisms that individuals of a cooperative species can use to increase overall dispersal success.

KEYWORDS
behavioural response, dispersal, faecal glucocorticoid metabolites, foraging, reproductive skew, *Suricata suricatta*, survival, vigilance

1 | INTRODUCTION

Dispersal is an important life-history trait, with consequences on gene flow and population dynamics (Bowler & Benton, 2005; Clobert et al., 2012). Throughout dispersal, individuals face several challenges and costs that can have important ramifications on their survival and reproduction (Bonte et al., 2012; Maag et al., 2019; Ridley, 2011; Soulsbury et al., 2008; Young et al., 2006). These challenges may, however, be overcome, or their negative effects reduced, through plastic behavioural adjustments (Bonte et al., 2012; Clobert et al., 2012). As such, understanding what influences time allocated to alternative behaviours and how such behaviours influence survival and reproduction is crucial to gaining a mechanistic understanding of the processes influencing dispersal success. However, mainly due to the difficulty of observing far-ranging individuals, little empirical information is available on the relationship between behavioural adjustment and demographic rates during dispersal.

Foraging, vigilance and aggression are undoubtedly among the most important behaviours influencing survival and reproductive output through resource acquisition, predator avoidance and, stress-related conception inhibition, respectively (Creel, 2001; Favreau et al., 2014; Hacklander et al., 2003; Watson et al., 2007). Where food resources are abundant, predictable and easily accessible, the required energetic intake can typically be fulfilled within relatively little time (Langvatn & Hanley, 1993; Stephens & Krebs, 1986) and survival should be higher than in stochastic and food-limited environments. A limited foraging time allows investment into complementary activities, such as vigilance. Vigilance has a positive effect on survival by reducing predation risk, and time allocated to vigilance has been shown to change according to the peaks of activity of predator species or to the number of eyes scanning for predators (Cowlishaw, 1998; Favreau et al., 2014). Successful foraging resulting in good body condition, not only enhances survival but it also has a positive effect on reproductive output (Weimerskirch, 2017). Particularly in social species, however, individual reproductive success is further influenced by within-group hierarchy-mediated aggressive interactions and the related stress (Hacklander et al., 2003; Sapolsky, 1985; Seebacher et al., 2013). For instance, the ability of a dominant female to aggressively control and dominate her subordinates has been proposed to cause skews in reproductive output (Clutton-Brock, 2001; Hacklander et al., 2003; Steenbeek, 1999).

Since one behaviour typically comes at the expenses of another, during the decision-making process individuals have to balance the costs and benefits of alternative activities (Favreau et al., 2014; Pays et al., 2011; Poysa, 1987). The time allocated to one or the other behaviour will thus depend on prevailing individual, social and environmental conditions and on the contribution of each behaviour towards key life-history processes (Poysa, 1987; Watson et al., 2007). Prevailing conditions, but also motivations and needs, differ between dispersing and resident individuals and throughout the different phases of the dispersal process (Bonte et al., 2012; Bowler & Benton, 2005; Cozzi et al., 2020), and so should the time, that is, allocated to alternative behaviours.

A population of habituated meerkats *Suricata suricatta*, part of a long-term behavioural and demographic study in the Kalahari Desert (Clutton-Brock & Manser, 2016), provides a unique opportunity to study individual, social and environmental correlates of behaviour during dispersal and their relationship with survival and reproduction. The long-term dataset further allows for a comparison of such relationships between resident and dispersing individuals. In resident meerkat groups, time allocated to foraging depends on the availability of food, which is influenced by habitat type and fluctuates seasonally according to rainfall (Doolan & Macdonald, 1996). Habitat type also influences time allocated to vigilance by offering different degrees of shelter from predators (Manser & Bell, 2004). Per capita time allocated to vigilance, which beside its anti-predator function also facilitates group cohesion during movements (Rauber & Manser, 2018), decreases with increasing group size (Clutton-Brock, Gaynor, et al., 1999). Additionally, foraging and vigilance vary as a consequence of individual-level factors, such as dominance and reproductive status (Clutton-Brock et al., 2004; Doolan & Macdonald, 1996; English, 2009). Dominant females are typically less involved in vigilance activities, and group members are more vigilant when pups are present in the group (Clutton-Brock, O'Riain, et al., 1999; Clutton-Brock et al., 2004; Doolan & Macdonald, 1996; English, 2009; Santema & Clutton-Brock, 2013). Survival and reproduction differ between dispersing and resident meerkats, but the underlying behavioural mechanism leading to such differences remains

largely unknown. Dispersing females have lower survival and reproductive rates than resident females (Maag, 2018), but their survival is not affected by dispersal distance (Maag et al., 2019). While subordinates in resident groups rarely reproduce (Bell et al., 2014; O'Riain et al., 2000; Young et al., 2006), subordinates in newly formed disperser groups have higher conception rates than their resident counterparts (Maag, 2018). This reduction in reproductive skew, which in long-established resident groups arises from a complex interaction between aggression from the dominant female and the associated increase in faecal glucocorticoid metabolite concentrations (fGCM), a stress-associated biomarker (Dantzer et al., 2016; Kutsukake & Clutton-Brock, 2005; Young et al., 2006), stems from the inability of a new dominant female to physically and physiologically suppress her subordinates at the start of tenure (Carlson et al., 2004; Clutton-Brock, 2001; Huchard et al., 2016; Russell et al., 2004).

Here, we used behavioural data collected on 67 dispersing and 108 resident meerkat females to investigate (a) which individual, social and environmental factors are associated with time allocated to foraging, vigilance and aggressive behaviour and (b) the relationship between these behaviours, and survival rate and reproductive output. We differentiated between dispersing and resident individuals and between the different phases of dispersal. Specifically, we expect time allocated to vigilance to decrease with increasing group size. In dispersers, vigilance may, however, be partly decoupled from group size due to its additional use in detecting potential mates, and we therefore predict differences in the effect of group size on vigilance between dispersers and residents. Additionally, we expect population density to have a stronger positive effect on vigilance in dispersers, as the risk of dispersers traversing occupied territory increases with a larger population. We expect time allocated to foraging to be higher during the transient phase of dispersal, due to increased energetic demand and limited knowledge of suitable foraging grounds, and to be lower pre- and post-transience. Across all dispersal phases, time allocated to foraging is expected to decrease during wetter times of the year when food availability is higher. Furthermore, as time allocated to foraging likely comes at the expense of time allocated to vigilance, we expect these behaviours to show opposing patterns across the different phases of the dispersal process. We expect that increased vigilance, at the expense of reduced foraging, will have a positive effect on survival during dispersal. Such effect should be more pronounced in dispersers than in residents, and particularly during the transient phase, as resident groups are more familiar with their surroundings and the associated risks. Lastly, we anticipate that aggression and fGCM concentrations will be similar between individuals in new disperser groups and individuals in established resident groups that experienced a recent change of dominance, but will be different from established groups where the dominant female has retained her position for a long time. We expect aggression by the dominant female and the associated stress to reflect differences in reproductive rates and reproductive skew between dispersers and residents. For instance, we anticipate conception skew between dominant and subordinate females to be less pronounced in both groups that experienced a recent change of dominance, and in new disperser groups, as compared to groups where the dominant female has retained her position for a long time. Similarly, we expect subordinates of resident groups where the dominant female has retained her position for a long time to have higher fGCM concentrations than subordinates in the other two group types.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted between 2013 and 2019 at the Kalahari Research Centre, Kuruman River Reserve (26°59′S, 21°50′E) in South Africa. The region is characterised by seasonal fluctuations in temperature and rainfall, with hot summers from October to April, when the majority of rainfall occurs, and cold, dry winters from May to September. The study area encompasses a variety of habitats including sparsely vegetated sand dunes, open salt pans and shrub/grassland plains (Cozzi et al., 2018; Appendix S3). The main predators for meerkats in this area are birds of prey such as martial eagles *Polemaetus bellicosus* and pale chanting goshawks *Melierax canorus*; however, predation pressure is relatively low (Clutton-Brock, Gaynor, et al., 1999). In this arid environment, food (e.g. arthropods and insect larvae) is generally scarce and patchily available after good rainfall (Clutton-Brock, Gaynor, et al., 1999). Between 8 and 12 resident meerkat groups, as well as several dispersing female coalitions have been monitored each year throughout the duration of this study. The choice of focusing on female dispersers was due to the predictability of their emigration from the natal group, following aggression by the dominant female. This enabled timely fitting of radio collars to regularly locate them during dispersal. For more information on the study site and long-term data collection, see Clutton-Brock and Manser (2016) for residents, and Cozzi et al. (2018), Maag et al. (2018) and Morales-González et al. (2019) for dispersers.

2.2 | Data collection

At least one female per dispersing coalition and per resident group carried a lightweight GPS (24 g; CDD Ltd, Greece) or VHF radio collar (23 g; Biotrack Ltd, Wareham, UK) allowing us to locate and visit each group to collect behavioural and life-history data (Clutton-Brock & Manser, 2016). Collars did not impact meerkat behaviour or survival and were fit to individuals while they were sedated using a mix of isofluorane and oxygen (Golabek et al., 2008), complying with appropriate regulations detailed in the Kalahari Meerkat Project protocol (Jordan et al., 2007). We did not collect any behavioural data or faecal samples within 24-hr post-anaesthesia.

We recorded behavioural data from dispersing and resident meerkats through individual focal follows, during which the focal individual was followed at a distance of a few meters and consecutive behaviours were recorded for 15–20 min. Recorded behaviours included resting; social activities such as grooming, pup provisioning, marking and excavating sleeping burrows; foraging and vigilance;

locomotion; and aggressive and competitive interactions between individuals and groups. The meerkats on site were habituated to human presence, which did not affect their behaviour (Clutton-Brock & Manser, 2016; Clutton-Brock et al., 1998). We followed individuals one to four times per week, avoiding the hot midday hours as meerkats typically rest during this time (Doolan & Macdonald, 1996). We took breaks of at least 20 min between follows in instances where an individual was followed more than once on the same day and considered each focal follow independent (Morales-González et al., 2019).

2.3 | Individual group types

We grouped followed individuals into two categories, *residents* and *dispersers*. We defined individuals as residents if they were part of an existing resident group, and as dispersers during the period between emigration from their natal resident group and 6 months after settlement in a new territory. We chose 6 months as our time interval to capture at least one full pregnancy (Sharp et al., 2012).

We subdivided resident and dispersing individuals into several group types. We subdivided resident individuals into *established dominant residents* (i.e. females that have held a dominant position in an existing resident group for longer than 6 months), *new dominant residents* (i.e. females that have acquired dominance within the last 6 months in an existing resident group) and *subordinate residents* (i.e. any non-dominant females older than one year). A detailed definition of dominance is given below. Distinguishing established dominant and new dominant residents was necessary, as different reproductive rates have been proposed to be linked to the ability of dominant females to suppress their subordinates (Clutton-Brock, 1998, 2001), and this ability changes over time (Huchard et al. 2016). This phenomenon has been observed in new dominant resident females during the first 3 months after dominance acquisition (Clutton-Brock, 2001). We extended this window to 6 months to allow the inclusion of at least one full pregnancy in all groups, including freshly settled dispersers. We divided the dispersal event in three phases: post-eviction, transience and settlement (see Appendix S1 for empirical characterisation of dispersal phases). We further subdivided dispersing individuals in *dominant dispersers* and *subordinate dispersers* (i.e. any female other than the dominant female).

To ease comparison between resident and dispersing individuals, we restricted data on residents to those that were collected during the period in which a dispersing coalition from that resident group was dispersing. This restriction acted to reduce temporal variability in environmental factors that we were unable to control for, such as seasonal variability in predation pressure.

2.4 | Foraging, vigilance and aggressive behaviour

We defined foraging behaviour as a composite of the following activities: scrabbling on the surface for small prey items such as insect eggs hidden immediately under the sand, scratching at multiple small holes on the surface to uncover larvae, actively digging larger holes to extract larger prey such as scorpions, and processing or eating food items (Chakravarty et al., 2019; Chakravarty et al., 2019; Rauber & Manser, 2017).

We aggregated three types of vigilance: bipedal vigilance (standing on hind legs and scanning the area), sitting vigilance (hind legs fully in contact with the ground) and guarding (raised vigilance >10 cm off the ground for at least 10 s; Roux et al., 2009). All three types of vigilance require a definitive stop to all other behaviours.

We differentiated between two types of aggressive interactions: counts of aggression initiated by a dominant female and received by female subordinates, and counts of spontaneous submission initiated by female subordinates and directed towards the dominant female (Kutsukake & Clutton-Brock, 2005).

2.5 | Measurement of faecal glucocorticoid metabolite concentrations (fGCM)

Quantification of fGCMs is a well-established, non-invasive approach to examine responses to stressors (Ganswindt et al., 2012). We opportunistically collected faecal samples immediately after defecation, stored them on ice and froze them at −18°C within 3 hr of collection. We lyophilised, pulverised and subsequently extracted 0.10–0.11 g of faecal powder by adding 3 ml of 80% watery methanol (Maag et al., 2019). We measured immunoreactive glucocorticoid metabolite concentrations from faecal extracts using a previously established group-specific enzyme immunoassay (Goncalves et al., 2016; Voellmy et al., 2014) detecting 3α 11β-Dihydroxy-CMs (Ganswindt et al., 2003; see Appendix S2 for further details).

2.6 | Individual, social and environmental factors

We determined the age of each individual born within the study population by observing pup emergence from the burrow at around 3 weeks of age (Clutton-Brock et al., 2008). We assigned dominance status (dominant or subordinate) based on the outcome of dyadic behavioural interactions where dominant individuals display aggressive assertive behaviour over subordinates, and subordinates submit in response (Thavarajah et al., 2014). We excluded from the analysis focal follows recorded before dominance was assigned. We assigned females who dispersed alone to their own social category—*lone*—and excluded them from aggression and fGCM analyses. We detected pregnancy status (pregnant or not pregnant) between 30 and 35 days into a 70-day gestation by visually inspecting individuals for enlarged abdomens (Doolan & Macdonald, 1996). We identified females as either lactating or not lactating by the presence or absence of dried sandy rings around their nipples (Sharp et al., 2012). We measured group size by counting the total number of adult (older than one year) meerkats present within a group on a given day, including both males and females. The date of birth was known for all individuals born within the study area (see above) and

individuals that had previously immigrated from outside the study area into resident groups were assumed to be adults. Group size ranged between 1 and 9 individuals in dispersing coalitions, and between 2 and 26 individuals in resident groups. We considered a focal follow to have occurred in the presence of dependent pups if the focal follow was conducted during the 90 days following their emergence (Bateman et al., 2013). We estimated density of the resident adult meerkat population during consecutive 2-month periods, following Paniw et al. (2019). We used the R package adehabitatHR (Calenge, 2006) and locations of sleeping burrows to calculate home-range sizes (for resident groups and recently settled dispersing coalitions) and from these the extent of the study area. We then divided the number of adults in the population (inferred through repeated visit of each group) by the extent of the study area. Density ranged from 1.39 to 5.67 meerkats per km^2. We determined the habitat type of each focal follow using a Landsat-derived vegetation map with five different habitat types (see Appendix S3 for methodological details and descriptions of the 5 habitat types; pans, drie-doring *Tribulius terrestris*, white sand mix, grasslands and red sand mix). We recorded hourly temperature and daily rainfall with on-site weather stations.

2.7 | Statistical analysis

We performed all statistical analyses in *R* (R Core Team, 2018). To investigate fixed and random effects, we used a variety of linear, generalised and Cox proportional hazard mixed-effects models detailed below. We nested individual identity within group identity as a random effect in all models to account for the non-independence of multiple observations from the same individual and group. We followed the same general procedure when constructing all linear and generalised mixed-effects models. We checked for over-dispersion using the package blmeco (Korner-Nievergelt et al., 2015), considering models with an over-dispersion parameter below 1.15 not to be over-dispersed (McCullagh & Nelder, 1994). We standardised all continuous covariates by subtracting the mean and dividing by the standard deviation. Using the package performance (Ldecke et al., 2019), we calculated a variance inflation factor for each covariate in all full models to test for collinearity; all values were below 3 indicating acceptably low levels of collinearity (Zuur, 2011). We assessed model assumptions by comparing standardised residuals to fitted values (Ferrari & Cribari-Neto, 2004). We included covariates in each model based on biological relevance to control for factors that have been shown or were expected to have an effect on each response (details are given below in each model). Visual data investigation did not show any obvious outliers. We selected the best model based on log-likelihood tests between candidate models to determine whether the removal of each covariate explained less variation (Harrison et al., 2018; for model selection AIC values, please see Appendix S5). When the removal of covariates did not change the explained variation, we chose the most parsimonious model (Burnham et al., 2010).

2.7.1 | Relationships between individual, social and environmental factors, and time spent foraging and vigilant

We obtained information on foraging and vigilance behaviours during 2,294 focal follows from 63 dispersers and 51 residents with an average of 25 (median = 15, range = 1–180) focal follows per individual (Appendix S6). Because the majority of behaviours last only a few seconds at a time (Chakravarty, Cozzi, et al., 2019), for each focal follow, we computed the proportion of time spent vigilant and foraging by dividing the cumulative amount of time spent in each of the two behaviours by the duration of the follow. Time spent foraging and vigilant were negatively associated ($r = -0.4$). However, given the vast number of alternative behaviours displayed by meerkats during each focal follow (see above), foraging and vigilance were not the complement of one other, and we therefore analysed them separately.

We built four generalised mixed-effects models with proportion of time allocated to foraging or vigilance behaviours during each focal follow as response variables: two models testing for differences among dispersal phases, and two models comparing dispersers and residents. With the package glmmTMB (Brooks et al., 2017), we used a beta-binomial distribution as the data were considerably over-dispersed (McCullagh & Nelder, 1994). In each model, we included age, dominance status, group size, population density, pregnancy status, lactation status, presence or absence of dependent pups, habitat type, cumulative rainfall from previous two weeks and maximum daily temperature as additional covariates. We further added two-way interaction terms to allow the effects of group size, presence or absence of pups and population density on the response variables to vary between dispersers and residents.

In the two models analysing differences between dispersers and residents, we pooled focal follows across all dispersal phases (post-eviction: 429 follows, transience: 271 settlement: 641). This is because we considered focal follows on residents from across the same time period as the whole dispersal event of interest (see *Individuals group type* section above) to control for external factors such as prey availability or predator density (which we cannot measure).

2.7.2 | Relationships between time spent foraging or vigilant and survival

To identify the effect of foraging and vigilance on survival, we investigated the fate of 67 dispersers and 83 residents and, using the package coxme (Therneau, 2019), created two mixed-effects cox proportional hazard models. The models investigated the effect of foraging and vigilance, respectively, on survival in dispersers and residents. We could not further differentiate between dominant and subordinate individuals due to the limited sample size. Here, the hazard rate $h[t]$ indicates the likelihood of an individual dying during an observation period (i.e. an entire dispersal event for dispersers and the corresponding time window for residents). We right censored individuals that were lost or still alive at the end of

an observation period (Fox & Weisberg, 2011). We included proportion of time spent foraging and vigilant (calculated for each individual across the period of interest) as explanatory variables. We controlled for age effects by including age at eviction as a covariate. By creating scaled Schoenfeld residual plots from the package survminer (Kassambara et al., 2019), we examined the assumption of proportional hazard. To visualise the results, we made these variables categorical by considering individual mean proportions above the global mean as 'high', and those below as 'low'.

2.7.3 | Reproductive rates and their relationship to aggressive behaviour and fGCM concentrations

We modelled conception probabilities by creating a discrete-step census (Ozgul et al., 2014; Paniw et al., 2019) to obtain monthly conception status, conditional on survival, within the study period for each female (1 or 0 if a female did or did not conceive). We recorded 1,452 monthly censuses repartitioned between dispersing coalitions (13 dominant and 38 subordinate individuals), resident groups with established dominant females (18 dominant and 110 subordinate individuals) and resident groups with new dominant females (9 dominant and 38 subordinate individuals). During these censuses, we detected 131 pregnancies. We only included dispersers that had settled in a new territory in this analysis, as pregnancies do not occur throughout emigration and transience. We compared conception probabilities between dominant and subordinate individuals of the three aforementioned group types (i.e. dispersing coalitions, resident groups with established dominant females and resident groups with new dominant females) using a generalised mixed-effects model with a binomial distribution (package glmmTMB; Brooks et al., 2017). Additional covariates for this model comprised group size and a two-way interaction term allowing the effect of dominance status to vary among the three group types.

Due to the resolution of data, namely the scarcity of aggression behaviours and infrequency of pregnancies, we were unable to formally test the relationship between aggression, fGCM and conception probability by including them in the same model. Instead, we created individual models investigating aggression and stress across the three group types. A parallelism between patterns of conception probability, and both aggression behaviours and fGCM concentrations (i.e. consistent differences between dispersers and residents across analyses), may suggest a direct relationship among aggression, stress and reproduction.

To test for differences in aggression and submission behaviours between individuals belonging to the three group types (i.e. dispersing coalitions, resident groups with an established dominant female and resident groups with a new dominant female), we built two generalised mixed-effects models with a negative binomial distribution (package lme4; Bates et al., 2015) using counts of aggression and submission behaviours, respectively, as response variables, and group size and pregnancy as explanatory covariates. We recorded aggressive interactions across 1,465 focal follows from 22 established dominant residents, 9 new dominant residents and 12 dominant dispersers with an average of 21 (median = 15, range = 1–151) focal follows per individual. We weighted each count according to the duration of the focal follow, to account for slight variations in focal observation durations.

To examine changes in fGCM levels between dominant and subordinate individuals across the three group types, we collected 758 faecal samples from dispersing coalitions (12 dominant and 19 subordinate individuals), resident groups with established dominant females (15 dominant and 59 subordinate individuals) and resident groups with new dominant females (8 dominant and 13 subordinate individuals), with a mean of 6 (median = 3, range = 1–34) samples per individual (additional information can be found in Appendix S6). We built a linear mixed-effects model with a Gaussian distribution (package lme4; Bates et al., 2015). The additional covariates we controlled for included the following: pregnancy, group size, sample collection time period (AM or PM), daily maximum temperature and a two-way interaction term allowing the effect of dominance status to vary among the three groups. Furthermore, we included counts of aggression initiated and submissions received by the dominant female within a group as covariates to explain stress levels of group members.

3 | RESULTS

3.1 | Relationships between individual, social and environmental factors, and time spent foraging and vigilant

During dispersal, time allocated to foraging increased from post-eviction to transience (slope: 0.45, $p < 0.001$) and into settlement (slope: 0.58, $p < 0.001$; Figure 1; Appendix S4). Vigilance decreased from post-eviction to transience (slope: −0.47, $p < 0.001$) and into settlement (slope: −0.77, $p < 0.001$; Figure 1; Appendix S4). When comparing dispersers to residents, the correlations between time spent foraging and vigilant, respectively, and group size differed (Figure 2; Table 1). Specifically, a one unit

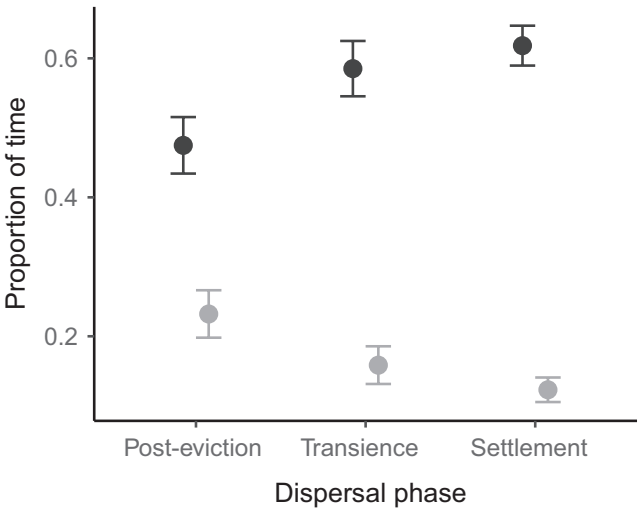

FIGURE 1 Proportion of time allocated to foraging (black) and vigilance (grey) behaviours across the three phases of dispersal in female meerkats. Error bars indicate 95% confidence intervals

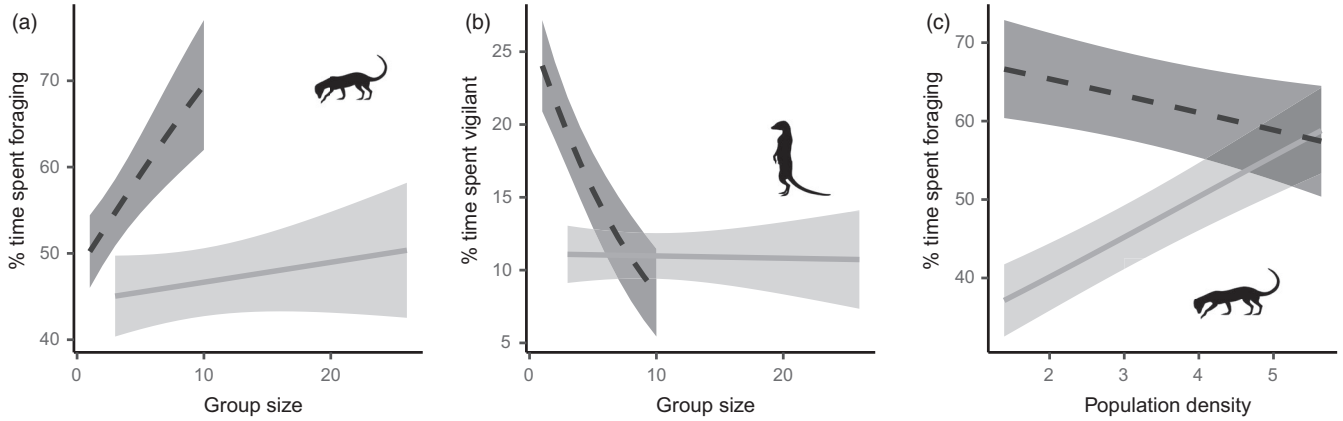

FIGURE 2 The effect of group size and population density on time spent foraging and vigilant in dispersing (dashed) and resident (solid) meerkats. Shading indicates 95% confidence intervals

TABLE 1 Relationship between individual, social and environmental factors on time spent foraging and vigilant in meerkats. For each model term, the slope, standard error (*SE*) and *p*-value are reported. Levels of a particular variable are indicated after the underscore, for example, *Category_Disperser*

Variable	Slope	*SE*	*p*
Foraging			
Category_Disperser	0.723	0.113	<0.001
GroupSize	0.043	0.038	0.266
PopulationDensity	0.194	0.030	<0.001
DailyMaxTemp	0.115	0.016	<0.001
TwoWeekRain	0.037	0.015	0.010
PresencePups_Present	−0.147	0.037	<0.001
Lactation_NotLactating	−0.132	0.038	<0.001
Category_Disperser:GroupSize	0.375	0.106	<0.001
Category_Disperser:PopDens	−0.280	0.044	<0.001
Vigilance			
Category_Disperser	0.115	0.127	0.365
GroupSize	−0.007	0.044	0.869
DailyMaxTemp	−0.101	0.019	<0.001
TwoWeekRain	−0.039	0.018	0.033
Age	−0.072	0.036	0.044
PresencePups_Present	0.077	0.044	0.084
Lactation_Lactating	0.141	0.046	0.002
Category_Disperser:GroupSize	−0.623	0.118	<0.001

increase in group size to a dispersing coalition had a stronger effect on time spent foraging than it had to a resident group (Figure 2). In addition, there was a decrease in per capita time spent vigilant for dispersers, but not for residents. Time spent foraging was strongly correlated with population density, and the interaction effect showed that such correlation differed between dispersers and residents (Figure 2). With increasing population density, time spent foraging decreased in dispersers and increased in residents. Population density did not affect time spent vigilant in either residents or dispersers. Moreover, time spent foraging was positively correlated with daily maximum temperature and cumulative rainfall over the previous 2 weeks, whereas time spent vigilant was negatively correlated with these factors (Table 1). In both dispersers and residents, time spent foraging correlated negatively with the presence of pups, whereas the opposite held true for vigilance (Table 1). Both foraging and vigilance were positively associated with lactation (Table 1). Habitat type did not correlate with time spent on either behaviour and was discarded during model selection.

3.2 | Relationships between time spent foraging or vigilant and survival

In both residents and dispersers, high proportions of foraging correlated with high survival (Figure 3a; Table 2). The interaction between category and foraging demonstrated that this correlation appeared to be stronger in dispersers compared to residents, despite not being supported statistically (Table 2). A similar overall trend was less obvious for vigilance: high proportions of vigilance correlated with lower survival in dispersers, yet the opposite applied for residents (Figure 3b).

3.3 | Reproductive rates and their relationship to aggressive behaviour and fGCM concentrations

The interaction effect between group type and dominance status indicated that subordinates from both resident groups (i.e. with established or new dominant females) had substantially lower probabilities of conceiving than their respective dominant female (Figure 4a; Table 3). In contrast, subordinates from dispersing groups had similar probabilities of conceiving as their respective dominant female, which lay between that of dominant and subordinate females of resident groups (Figure 4a; Table 3). Aggression initiated by dominant females towards their female subordinates did not vary between dispersers or between either resident groups. There was a weak positive

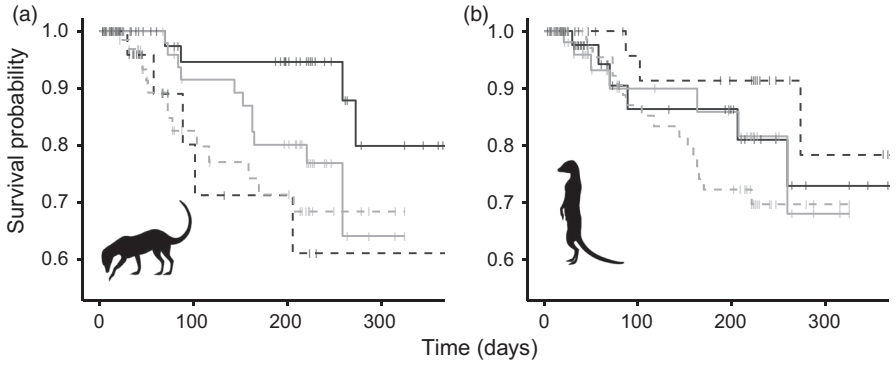

FIGURE 3 Kaplan–Meier curves showing the relationship between high (solid lines) and low (dashed lines) foraging (panel a) and vigilance (b) behaviours, and the survival probabilities of dispersing (black lines) and resident (grey lines) meerkats. Ticks along the lines indicate censored individuals

TABLE 2 Effects of mean proportion of time allocated to foraging and vigilance behaviour on survival probabilities of dispersing and resident meerkats. For each model term, the slope, hazard ratio, standard error (*SE*), 95% confidence intervals (CI) and *p*-value are reported. Levels of a particular variable are indicated after the underscore, for example, *Category_Resident*

Survival models	Slope	Hazard ratio	*SE*	Lower CI	Upper CI	*p*
Foraging						
MeanForagingProportion	−9.047	0.001	3.440	−15.789	−2.305	0.009
Category_Resident	−0.513	0.599	1.679	−3.804	2.778	0.760
Age	0.001	1.000	0.001	−0.001	0.003	0.630
MeanForagingProportion:Category_Resident	2.385	10. 862	3.124	−3.738	8.508	0.450
Vigilance						
MeanVigilanceProportion	9.433	12,491.2	3.796	1.993	16.873	0.013
Category_Resident	1.702	5.483	0.884	−0.031	3.435	0.054
Age	0.001	1.000	0.001	−0.001	0.003	0.530
MeanVigilanceProportion:Category_Resident	−3.674	0.025	3.359	−10.258	2.910	0.270

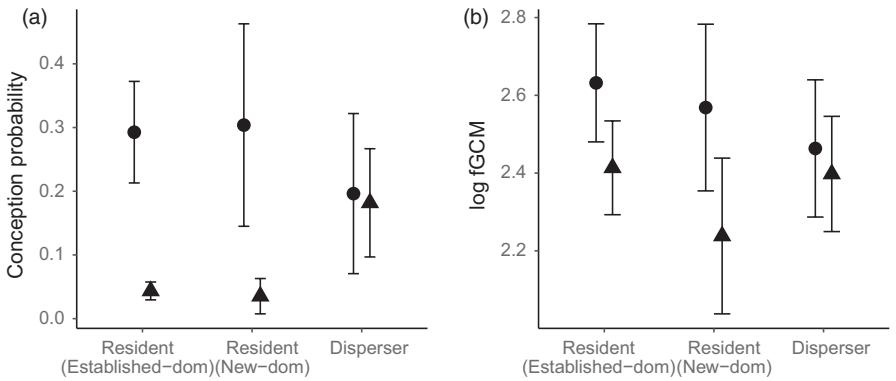

FIGURE 4 Monthly conception probabilities (a) and log faecal glucocorticoid metabolite (fGCM) concentrations (b) for dominant (circles) and subordinate (triangles) females in newly formed dispersing groups (Disperser) and resident groups with long-established (Established) and new (New) dominant females. Error bars indicate 95% confidence intervals

correlation between group size and aggression behaviours across all three group types (Table 3). Submissions by subordinates towards their dominant female did not vary between the three group types. Submissions were, however, positively correlated with pregnancy of the dominant female irrespective of group type (Table 3).

Visual inspection of model predictions (specifically the interaction between group type and dominance status) showed that in both resident groups (i.e. with established and new dominants), fGCM concentrations of subordinate females were lower than those of dominant females (Figure 4b). In dispersing groups, however, there was no difference in fGCM concentrations between dominant and subordinate females (Figure 4b). Among all three group types, pregnancy was positively correlated with fGCM concentration while group size was negatively correlated. Including aggression and submissions as predictor variables did not explain any further variation in fGCM concentration.

4 | DISCUSSION

Behavioural responses to the same individual, social and environmental stressors varied between dispersing and resident individuals. Similarly, the relationship between behaviour and both survival and

TABLE 3 Relationship between individual, social and environmental factors on conception probabilities, aggression and submission behaviours, and fGCM concentrations of meerkats. For each model term, the slope, standard error (*SE*) and *p*-value are reported. Levels of a particular variable are indicated after the underscore, for example, *GroupType_Disperser*

Model	Slope	*SE*	*p*
Conception			
GroupType_ResNewDom	0.581	0.548	0.289
GroupType_ResEstablishedDom	0.527	0.448	0.239
DomStatus_Subordinate	−0.095	0.408	0.816
GroupSize	−0.197	0.132	0.136
DomStatus_Subordinate:GroupType_ResNewDom	−2.386	0.697	<0.001
DomStatus_Subordinate:GroupType_ResEstablishedDom	−2.114	0.484	<0.001
Aggression			
GroupType_ResNewDom	0.711	0.961	0.460
GroupType_ResEstablishedDom	−0.927	0.919	0.313
GroupSize	0.391	0.216	0.070
Pregnancy_Pregnant	0.053	0.297	0.857
Submission			
GroupType_ResNewDom	1.076	0.782	0.169
GroupType_ResEstablishedDom	0.128	0.748	0.864
GroupSize	0.137	0.169	0.418
Pregnancy_Pregnant	1.020	0.251	<0.001
fGCM			
GroupType_ResNewDom	0.105	0.133	0.431
GroupType_ResEstablishedDom	0.169	0.113	0.139
DomStatus_Subordinate	−0.066	0.086	0.447
GroupSize	−0.096	0.028	<0.001
Pregnancy_Pregnant	0.133	0.040	<0.01
DailyMaxTemp	−0.089	0.016	<0.001
Collection_PM	−0.164	0.031	<0.001
GroupType_ResNewDom:DomStatus_Subordinate	−0.265	0.139	0.058
GroupType_ResEstablishedDom:DomStatus_Subordinate	−0.153	0.105	0.150

reproductive output varied between dispersers and residents. Survival during dispersal was positively correlated to increasing time spent foraging, rather than vigilant. Furthermore, we observed similar levels of adrenocortical activity between dominant and subordinate females of newly formed dispersing groups. We suggest this to be a possible explanation for the observed reduction in reproductive skew in dispersers as patterns of conception probabilities reflected fGCM levels across strategies (dispersers and residents). The observed relationships between behaviour, survival and reproduction provide us with a possible mechanistic understanding of the processes influencing important demographic rates during dispersal rates which determine overall dispersal success.

4.1 | Relationships between individual, social and environmental factors, and time spent foraging and vigilant

Time allocated to foraging and vigilance increased and decreased, respectively, across the three phases of dispersal, supporting the idea that dispersers experience differing challenges and constraints in each phase (Bowler & Benton, 2005; Cozzi et al., 2020; Maag et al., 2019). We showed that time allocated to foraging increased and time allocated to vigilance decreased with increasing group size in dispersers, this result was in line with previous studies and characteristic of cooperative breeders (Clutton-Brock, Gaynor, et al., 1999; Quenette, 1990; Ridley, 2011; Young, 2003). However, we did not find such effect in residents. Where other studies have looked specifically at guarding behaviour (Clutton-Brock, Gaynor, et al., 1999), we analysed a composite of vigilance behaviours, and speculate that guarding alone may act as predator awareness, whereas other measures of vigilance, as included here, may serve additional purposes such as locating group members or avoiding aggressive interactions. Within the size range of dispersing groups (1–9 individuals), both time allocated to foraging and to vigilance were consistently higher in dispersers, suggesting less time was allocated to alternative behaviours, such as social interactions. The overall higher time allocated to vigilance in dispersers compared to residents was possibly due to a higher perceived risk associated with unfamiliarity of the surroundings. Vigilance, however, rapidly decreased for every additional group member in dispersers to the benefit of time allocated to foraging. This is indicative of the dispersers' priority to maximise foraging where possible, for example when group size allows. Increasing foraging may be a behavioural response to increase

dispersal success, as corroborated by our results showing that a high level of foraging is directly associated with higher survival.

Social circumstances had a considerable effect on behaviour in both dispersers and residents. Surprisingly, while several mammal species are characterised by an increase in time spent foraging (e.g. Columbian ground squirrels *Urocitellus columbianus*: Macwhirter, 1991) and a decrease in vigilance when lactating and providing for young (e.g. plains zebra *Equus burchelli* and chacma baboons *Papio ursinus*: Barnier et al., 2016; Barrett et al., 2006), we found that time allocated to both behaviours increased. The increase in foraging is likely to compensate for the considerable energy cost associated with lactating (Doolan & Macdonald) and the increase in vigilance is crucial for locating potential threats to vulnerable pups (Dyble et al., 2019). As both behaviours increased, this likely occurs at a cost to the maintenance of other social behaviours. Against expectations, the decrease in disperser foraging proportions with increasing population density is likely because with a larger population, dispersers must engage with more social signals, such as scent marking. We are unsure how to explain the opposite correlation in residents. We suggest that the increase in foraging with increasing group size may be an artefact of better food availability, which facilitates a larger population.

Environmental factors played only a minor role in determining behaviour. Foraging behaviour increased with increasing cumulative rainfall and daily maximum temperatures, reflecting increased accessibility of prey items under these environmental conditions (Doolan & Macdonald, 1996). Furthermore, the increase in time allocated to foraging behaviour with increasing temperatures may act as compensation for the longer midday rest periods taken on hotter days (de Ven et al., 2019).

The effect of social circumstances on both behaviours and the absence of a relationship between habitat type and foraging or vigilance support past studies showing that, in dispersing meerkats, social circumstances influence aspects of behaviour more so than habitat characteristics (Cozzi et al., 2018; Morales-González et al., 2019). Nonetheless, we cannot rule out that the absence of an effect of habitat type on behaviour may be due to a misrepresentation of the landscape as perceived by dispersers. For instance, we lacked information on prey densities and predation pressure among the five habitat types, factors that likely influence time allocated to foraging and vigilance.

4.2 | Relationships between time spent foraging or vigilant and survival

Against expectations, we observed a positive relationship between time spent foraging, instead of time spent vigilant, and survival. This suggests that as in other species like the grey partridge *Perdix perdix*, foraging and the resulting maintenance of body condition are more important to long-term survival than vigilance and the associated anti-predator behaviour (Watson et al., 2007). This may be particularly true in environments such as our study area, where predation pressure is low and food generally scarce (Clutton-Brock, Gaynor, et al., 1999), and environmental conditions are seasonal and harsh (Paniw et al., 2019). Particularly in dispersers, who suffer deterioration of body condition more so than residents (Maag et al., 2019), maximising time spent foraging, at the expenses of vigilance and other behaviours, might be a strategy to increase survival. Our results, which hint at a stronger relationship between foraging and survival in dispersers than in residents, support this hypothesis. While our visual model predictions suggest a potential difference in the magnitude of the behavioural effects on survival, this difference was not statistically apparent, potentially due to our low sample size, and would therefore become clearer with future research on a larger dataset. Moreover, additional factors from our analysis in part (a) may mediate any influence of foraging and vigilance behaviours on survival through their effects on time allocated to foraging and vigilance, for example, through its positive effect on time spent foraging, group size may mediate the effect of foraging on survival.

The seemingly counterintuitive reduction of survival with increasing time allocated to vigilance observed in dispersers may be the consequence of the environment through which a dispersal event takes place. For instance, high levels of vigilance may indicate that a dispersing individual/coalition moves through a hazardous and risky environment, such as one with high predation pressure, where it would naturally experience lower survival. Dispersers are unfamiliar with the area and have limited knowledge of shelter location, which may also induce higher vigilance, and decrease the probability of successful escape from predators (Manser & Bell, 2004).

4.3 | Reproductive rates and their relationship to aggressive behaviour and fGCM concentrations

It has been suggested that an increase in reproductive output in subordinates results from the inability of new dominant females to suppress their reproduction, and that such inability is linked to experience and other physiological mechanisms (Clutton-Brock, 2001; Huchard et al., 2016). Levels of fGCM have been studied substantially in meerkats (Maag et al., 2019; Young, 2003), however, we provide novel findings by subdividing resident individuals into groups with either new or established dominant females. While we observed an increase in reproductive output by subordinate females in newly formed dispersing groups, we did not observe the same pattern for subordinate females in resident groups with a new dominant female. In the latter groups, reproductive skew between dominants and subordinates was instead similar to that of resident groups with established dominant females. Our findings thus suggest that consolidation of dominance to levels reflecting those of established dominant females requires a longer period in newly formed dispersing groups compared to resident groups that experienced a recent change in dominance. Additionally, dominant females in newly formed dispersing groups may be more 'permissive' towards their subordinates to increase group cohesion in the early stages. Moreover, the higher reproductive output observed in subordinate

females of newly formed dispersing groups might help to explain why individuals take on the challenges of dispersing after eviction despite the (undesirable) concrete possibility of transitioning from a subordinate position in the natal group (where they are full sibs to newborns) to a subordinate position in the newly formed group (where they are aunts to newborns). The possibility of obtaining dominance or, alternatively, the direct fitness benefits experienced as a subordinate during the first months after group formation may counterbalance the physical costs of dispersal and the loss of indirect and direct fitness (Bonte et al. 2012; Maag et al., 2019). This finding is likely transferrable to other cooperatively breeding species, helping to more accurately quantify the costs and benefits of dispersal.

The similarity in pattern we found between conception probabilities and fGCM concentrations (differences between dispersers and both resident group types were consistent across both analyses) suggests that like other species, such as alpine marmots *Marmota marmota* (Hacklander et al., 2003), reproductive rates are mediated by the effects of stress (glucocorticoids). Lastly, inbreeding avoidance (O'Riain et al., 2000) may further drive the pattern of reproductive skew observed. In resident groups, the majority of subordinate females are direct descendants of the dominant male (Clutton-Brock et al., 2004), which is not the case for newly formed dispersing groups where all males are initially unrelated to all females.

5 | CONCLUSIONS

We showed that through the effect of individual, social and environmental factors, differential behavioural responses can mediate demographic rates. Individual and social factors in particular correlated with time allocated to foraging and vigilance, and the relationship between these factors and behaviours varied between dispersers and residents. Time allocated to foraging, rather than vigilance, was linked to high survival. While we did not formally test for an association between aggression or fGCM concentrations and reproduction, the fact that patterns of conception rates were mirrored by patterns of fGCM concentrations may suggest a relationship between stress and reproduction. Our results shed some light on the behavioural and physiological mechanisms by which dispersers may reduce mortality and maximise direct reproductive output. The results of our study pave the way towards a complete mechanistic and conceptual understanding of the dispersal process and its broader implications for population dynamics.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

N.D.H., N.M., A.O. and G.C. conceived the study; N.D.H. and N.M. collected the data on dispersing individuals, and T.H.C.-B. and M.B.M. led the collection of data on resident groups; A.G. led the steroid extraction and analysis, and P.J.H. contributed the habitat map; N.D.H. performed statistical modelling and wrote the manuscript; N.M., A.O. and G.C. consulted on statistical modelling. All authors substantially contributed to the final draft. The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.70rxwdbxz (Harrison et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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